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A STUDY OF MEIOSIS IN A HAPLOID OF *TRITICUM VULGARE* AND ITS PROGENIES

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THE UNIVERSITY OF ALBERTA

A STUDY OF MEIOSIS IN A HAPLOID OF TRITICUM VULGARE AND ITS PROGENIES

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ABSTRACT

A study was conducted on the meiotic behaviour of a 21 chromosome haploid of Triticum vulgare and its progenies.

Metaphase I and anaphase I of meiosis were not clearly differentiated, but chromosome counts were made when the univalents had migrated to the poles. Random distribution to the poles was apparently restricted by the presence of true bivalents and secondary pairing. When no pairing occurred, the distribution of univalents appeared random.

One, two or three bivalents were present in 67.5% of the cells counted. The presence of true bivalents indicated considerable homology between chromosomes not normally considered homologous. No bridges or fragments were observed.

A few cells contained a completely reduplicated set of chromosomes. In these cases, 42 chromosomes were present. It is believed that chromosome doubling with failure of cell wall formation in a sporogenous cell prior to microsporocyte formation, resulted in the duplications observed.

Chains of 3, 4, and 5, were observed in the haploid. These associations appeared as continuations of secondary pairing.

The F_2 and F_3 generations were studied cytologically. Although a high frequency of aberrations was observed, a general trend toward a normal complement of chromosomes was indicated in later generations. Univalents, trivalents and quadrivalents were the most frequent aberrations. It is postulated that crossing-over between partially homologous chromosomes in the haploid resulted in reciprocal translocations which were transmitted to succeeding generations. Deficient and duplicated gametes resulting from such translocations probably gave rise to aneuploid plants with various types of associations in later generations.

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A STUDY OF MEIOSIS IN A HAPLOID OF *TRITICUM VULGARE* AND ITS PROGENIES

R. C. McGinnis

INTRODUCTION

A haploid plant contains the gametic number or only half the normal chromosome complement. Haploids are usually somewhat dwarfed and less vigorous than their sister diploids, and their reproductive organs are correspondingly reduced in size. They occur rarely in most species under natural conditions, and presumably arise from parthenogenic development of an egg cell or an accompanying synergid.

Because of the aberrant chromosomal behaviour during meiosis, haploids are generally highly sterile. Theoretically however, they need not be completely sterile, for no matter how many chromosomes a species may have, a certain percentage of the eggs and sperms should contain a haploid set of chromosomes.

Union of such gametes would give rise to a diploid plant which would be completely homozygous for all characters. Diploids could also be obtained from haploids by the union of unreduced gametes. Such diploid plants would be of considerable value for studying the genetics of quantitative characters.

Haploids have been of interest in the study of the phylogeny of a species. Cytological observations of the extent of chromosome pairing tendencies in haploids, have given information concerning basic chromosome numbers and relationships in the species studied.

A practical application of haploidy has recently been demonstrated with the derivation of monosomic lines in common wheat. Monosomics in turn, have been found of value in associating certain genes with specific chromosomes and may also prove to be useful for transferring inherited characteristics by a method of chromosome substitution from one variety to another.

In Triticum vulgare, haploids are primarily of interest in a study of chromosomal associations between genomes, and the meiotic behaviour of unpaired chromosomes. Aberrations involving whole chromosome deficiencies or duplications, and reciprocal translocations observed in the progeny of haploids, make possible a more complete study of linkage and inheritance in this species.

In this paper the results of cytological investigations of chromosome behaviour at meiosis of a haploid of Triticum vulgare and its progenies are presented and discussed.

LITERATURE REVIEW

Occurrence

Work on haploid plants has become prominent only in recent years and records of haploidy are still rare. The first haploid seed plant was described by Blakeslee, et al (1), in 1922. Two such plants appeared in the offspring of normal Datura plants which had been subjected to low temperatures at the time of fertilization. Since this initial work by Blakeslee, et al (1), haploids have been found from time to time and described in about 20 genera of plants.

Origin

There has been much speculation as to the origin of haploids. According to Cooper (3), Harland (8), and Muntzing (19), poly-embryony or twin-seedlings appeared to be one of the more frequent sources. Harland (8), in a germination experiment with Sea Island cotton, observed 20 seeds containing two embryos, one of which was usually much larger than the other. From such material 16 pairs of plants were raised to maturity; of these 14 pairs consisted of one haploid and one diploid, and two pairs each of identical diploids. Cooper (3) observed a number of haploid-diploid twins in Lillium and Nicotiana. He suggested that this phenomenon occurs when a synergid is stimulated to divide and that many of the haploid plants discovered arise from synergids.

Crosses between distantly related species have in a few instances given rise to haploids. Gaines and Aase (7) obtained a haploid with 21 chromosomes by pollinating a winter wheat, Triticum compactum humboldii with the pollen of Aegilops cylindrica. In this cross, usually only shrivelled seeds resulted but the single plump kernel which produced the haploid was much larger than seed of the Triticum parent.

Gaines and Aase (7), suggested that both generative nuclei of the Aegilops pollen fused with the maternal endosperm nuclei to produce a tetraploid endosperm, while the egg developed parthenogenically. Smith (23), discussing wide crosses such as the one described by Gaines and Aase (7), postulated that, "possibly the endosperm with two maternal and one paternal set of chromosomes is capable of developing; but the embryo with one maternal and one paternal set dies, in which event a synergid or an already partially developed maternal embryo, develops into a haploid embryo".

Various artificial methods have been employed in producing haploids. Cold treatment was used by Blakeslee, et al (1), in Datura. It was postulated that the low temperature caused the parthenogenic development of the egg cells. Ivanov (9), Katayama (10), Kihara and Katayama (12), Kihara and Yamashita (13), Kostoff (14), and Smith (23), have attempted the production of haploids by the use of X-rays. Ivanov (9) believed that X-rayed pollen produced a significant increase in the number of haploids in Nicotiana rustica var. humilis. His work was corroborated by Kostoff (14) on similar material. Katayama (10), Kihara and Katayama (12), and Kihara and Yamashita (13) obtained significant increases in the incidence of haploidy in einkorn from the use of X-rayed pollen. Smith (23), however, found no increase in

einkorn haploids from X-rayed pollen. Actually fewer haploids were obtained in one experiment when such treated pollen was used.

Delayed pollination has been used as a means of increasing the occurrence of haploid plants. Kihara (11) reported that if pollination of einkorn wheat was delayed beyond the normal time after emasculation, the frequency of haploids was correlated (to a point) with the length of the delay. He also observed three pairs of twin seedlings which presumably arose from delayed pollination.

Lindstrom (17) described a tomato mutant which had 12 chromosomes. It appeared in the F_2 population of a varietal cross and showed complete fertility. Lindstrom (17), regarded this haploid as "spontaneous", as no apparent stimulus was responsible for its production.

Meiotic Behaviour

Meiotic behaviour of haploids has been studied by a number of workers; (2), (4), (5), (6), (7), (9), (15), (16), (17), (18), (20), (23), and (25). To date there is no

general agreement since each species has apparently somewhat different meiotic characteristics.

Random distribution of the chromosomes to the poles was observed by Bleier (2), Davis and Kulkarni (4), Gaines and Aase (7), Ivanov (9), and Tometorp (25). Gaines and Aase (7) found that pairing occurred only rarely in their 21 chromosome wheat plant. The chromosomes apparently were distributed to the poles at random. Davis and Kulkarni (4) in their studies of an Oenothera francisca haploid, found that none of the seven chromosomes paired. Sterile pollen resulted from the irregular distribution of the chromosomes in the first division; (6+1), (5+2), and (4+3). They postulated that functional pollen grains resulted when a unipolar spindle had formed and all seven chromosomes were drawn to one pole. Ivanov (9) studied a haploid of Nicotiana rustica and observed that chromosome pairing was almost entirely absent. At metaphase I the chromosomes lay scattered over the entire spindle.

In some Matthiola hybrids, Lesley and Frost (15) obtained a haploid which had seven univalents plus a fragment. No pairing was observed. In some cases, random distribution of the unpaired chromosomes occurred, but frequently the chromosomes split and separated. In these cases the first division was evidently omitted and pollen dyads resulted.

Emerson (5) studied a haploid of Oe. francisca but did not observe the same behaviour as that described by Davis and Kulkarni (4). He observed two chromosomes frequently attached end-to-end. The behaviour of these two chromosomes apparently differed from that of the other five univalents. In early anaphase I, the members of the pair usually passed to opposite poles while the other five univalent chromosomes were distributed at random. Counts of the chromosomes in the two daughter nuclei showed the following distributions; 7 cases (7+0), 25 cases (6+1), 18 cases (5+2) and 15 cases (4+3). Emerson concluded that the high frequency of the (6+1) distribution was the result of the frequent movement to one pole of all five univalents, with one member of the dividing pair.

Recently, instances of chromosome pairing in haploids have been reported, (2, 6, 14, 16, 18, 20, 23, and 26). These workers however, do not agree in their definitions of chromosome pairing nor in their interpretations of its significance.

Levan (16), who studied meiosis in haploid rye, occasionally found two bivalents and one trivalent at diakinesis. The presence of numerous chiasmata apparently held paired chromosomes together even to metaphase I. He did not believe that chiasmata could form between non-homologous chromosome portions and therefore concluded that pairing was between chromosomes that

were actually partially homologous. Kostoff (14) was of the opinion that in haploid einkorn, pairing had nothing to do with chromosome homology but occurred between inert heterochromatic regions.

Yamasaki (26), in a Triticum vulgare haploid, observed the following pairing frequencies at metaphase I; 21' - 47.7%, 19'1" - 37.1%, 17'2" - 12.4%, 15'3" - 2.4%, and 13'4" - 0.4%. An occasional trivalent was also noted and taken as an indication that a relationship existed among the three genomes.

Smith (23) found a low percentage of open bivalents with observable chiasmata in einkorn haploids. More frequently, however, he found chromosomes arranged at first metaphase so that they might be considered as two secondary pairs. He suggested that this might be taken as evidence that five is the basic number of chromosomes in wheat. Smith (23) considered two chromosomes as secondary pairs if they were not more than the diameter of a chromosome apart at any one point. Only a small number were paired throughout their entire length.

In Arctic Grass haploids, Flovic (6) concluded that real homology involves the exchange of chromatin and secondary pairing may occur as a result of phylogenetic affinity of chromosomes without intimate homology. He pointed out that secondary pairing may be caused by mutations or structural changes of the chromosomes, but is probably evidence of a lower basic number.

Nordenskiold (20), in a haploid rye plant, observed a bivalent in 3.2% of the pollen mother cells which were cytologically examined. This bivalent was always rod-shaped and appeared to be joined by a chiasma. Bleier (2) suggested that bivalent formation is not constant in haploids and that factors other than strict homology (e.g. the chance sticking together of chromosomes from prophase on), have a greater influence on pairing.

Morinage and Fukushima (18) studied meiosis in a haploid rice plant and found that pollen mother cells contained one or two bivalents. Those at the equator were considered as true bivalents. Tomtorp (25) found that a bivalent was formed in 5% of the pollen mother cells of a Hordeum distichum haploid. He did not believe that bivalents are a secondary phenomenon but that they may arise through relic similarity of chromosomes.

The appearance of chromosome bridges at first or second anaphase of haploids has been reported by a number of investigators. Levan (16) frequently observed chromatin bridges without fragments in a rye haploid. He suggested that their presence could result from chromatid reunion. Katayama (10) and Smith (23), working independently, observed bridges in einkorn haploids which had fragments occasionally associated with them. Smith (23) found a high correlation between the number of bivalents and the number of bridges. He pointed out that these

bridges probably resulted from crossing-over between non-homologous chromosomes and, "if this interpretation is applicable to the bridges in haploid einkorn, it would suggest that crossing-over had occurred between most of the bivalents. ..... it thus follows that true chiasmata were observed".

To date, Sears (21) has made the most practical use of a haploid plant. He obtained two haploids from the cross T. vulgare pollinated by Secale cereale. When pollinated with normal wheat pollen, one plant produced 14 seeds and from these, 13 plants matured. These plants and their progeny were examined cytologically, and Sears (21) observed 11 plants with an aberrant chromosomal complement. Univalents, trivalents and rings of four were found in conjunction with normal bivalents. Since Sears (21) was unable to examine the original haploid cytologically, he could only postulate the probable cause of the aberrations (monosomics, trisomics, etc.), observed in the F_1 and subsequent generations.

MATERIALS AND METHODS

In July, 1949, a haploid of Triticum vulgare was observed in an F_3 experimental plot of the inter-varietal cross, Lemhi x (Bunyip x Dicklow). It was not noticed until flowering time when the spreading of the glumes, characteristic of sterility, drew attention to it. It is not believed that the haploid arose through twin embryos as only one plant was present. Three slightly dwarfed and spindly tillers were present; two in flower and the third young enough to allow cytological examination of the pollen mother cells. This spike was removed and fixed for cytological studies.

Of the two remaining spikes, one was allowed to self-pollinate while the second was emasculated and pollinated with normal Lemhi pollen. Emasculation was probably unnecessary since the selfed spike proved to be completely sterile. Heavy rains in mid-July, stimulated the formation of two more tillers which were also emasculated and pollinated with Lemhi pollen. The three cross-pollinated spikes produced eight seeds.

The eight seeds from the haploid were sown in the greenhouse in September, 1949, and seven F_1 progenies were obtained Unfortunately greenhouse conditions were poor during the germination and tillering periods, and only one spike per plant was

produced. Consequently the chromosome complement could not be obtained without eliminating subsequent generations. Of the seven F_1 plants, only one proved to be completely sterile and it has been suggested that high temperatures in the greenhouse during the flowering period may have been partially responsible.

Ten seeds of each of 18 sister plants to the haploid were also seeded in the greenhouse in September, 1949, in progeny lines. Six plants in each line were studied cytologically so that the chromosome makeup of the immediate parent of the haploid could be determined.

The F_2 and F_3 generations from the haploid were planted in progeny lines in the greenhouse in February and June, 1950, respectively. Only a small percentage of these plants failed to survive. Each plant produced several tillers and cytological studies of microsporogenisis were made on all plants.

In this study, all plant material to be examined cytologically was fixed in 6:3:1 Carnoy's fluid A, and the acetocarmine smear method as outlined by Smith (24) was used for slide preparations. Chromosome counts were made at a magnification of 600 diameters and photomicrographs were taken at a magnification of either 720 or 900 diameters. The tertiary butyl alcohol method, as outlined by Smith (24), was used for making slides permanent.

EXPERIMENTAL RESULTS AND INTERPRETATIONS

CYTOLOGICAL DATA FROM THE HAPLOID PLANT

Distribution of Univalent Chromosomes

In general the chromosomes were distributed throughout the entire cell at metaphase I, as can be seen in Figs. 1 and 2. This observation is in agreement with the work of Bleier (2), Gaines and Aase (7), Ivanov (9), and other workers. Apparently the univalents did not line up on the plate prior to the first anaphase as do normal bivalents. Consequently these two phases were not clearly distinguishable.

A total of 274 pollen mother cells were counted in which the univalents had migrated to the poles, Figs. 3, 4, and 5. The anaphase I distributions are presented in Table 1.

Table 1

Distribution of Univalents

Distribution	20-1	19-2	18-3	17-4	16-5	15-6	14-7	13-8	12-9	11-10	Total
No. of cells	2	2	7	2	15	8	31	19	90	98	274
% of total	0.7	0.7	2.6	0.7	5.5	2.9	11.3	6.9	32.9	35.8	100%
Normal (%) distribution	0.002	0.02	0.1	0.6	1.9	5.2	11.1	19.4	28.0	33.6	100%
X^2	245.000**	23.120**	62.500**	0.017	6.821**	1.017	--	8.054**	0.858	0.144	347.531

** Highly significant.

Cells with near equal distribution occurred with the highest frequencies. Actually the 11-10, 12-9, 14-7, 15-6, and 17-4 distribution values were fairly close to the expected values for random distribution. Some of the other distributions, however, deviated very markedly from the expected so that for the entire study a highly significant X^2 was obtained. It was quite apparent, therefore, that randomness of distribution to the poles was restricted. It is interesting that a 20-1 distribution was observed in two of the cells studied, Fig. 5. Sears (21), in one of his papers, postulated that such a gamete could be one possible source of monosomic wheat plants.

Chromosome Associations

Paired Chromosomes

A large number of cells with paired chromosomes were observed. True pairing was assumed if a chiasma was actually observed, Fig. 6, or if the tapered end appearance of a disjoining pair indicated the previous existence of a chiasma. So-called secondary pairing was also frequently noted, consisting merely of an end-to-end association of univalent chromosomes with no sign of a real chiasma, Fig. 2. The data on bivalent and other association frequencies are summarized in Table 2.

Table 2

Chromosome Associations

Association	21'	19'1"	17'2"	15'3"	21"	42'	21 dyads	Chain of 3	Chain of 4	Chain of 5	Total
No. of cells	93	117	115	23	1	7	5	11	5	1	378
% of total	24.6	31.0	30.4	6.1	0.3	1.8	1.3	2.9	1.3	0.3	100

Of a total of 378 pollen mother cells counted at metaphase I, the greatest proportion (31.0% and 30.4%) had a constitution of 19'1" and 17'2", respectively. A constitution of 15'3" was observed in 6.1% of the cells, but no cell was observed that had more than three pairs. These frequencies are quite different from those reported by Yamasaki (26).

The cause of bivalent pairing in the haploid could have two interpretations. Had the parent of the haploid been heterozygous for a number of reciprocal translocations, bivalent formation in the haploid could be expected. On the other hand, pairing would also occur if there were homology between various chromosomes in the haploid. The first hypothesis can be ruled out since no ring or chain associations were found in the progenies of the haploid sister plants. All 108 sister progenies proved to be completely normal cytologically. The pairing observed must, therefore, be taken as evidence of true homology between certain of the haploid chromosomes resulting in the occurrence of reciprocal translocations between these chromosomes. If the presence of bivalents is a true measure of the number of reciprocal translocations that have taken place, it can be assumed that up to three such exchanges have occurred in some cells. It is not suspected that this homology was between chromosomes of the same genome, but rather between chromosomes of different genomes. Smith (23)

observed a low frequency of bivalents in einkorn haploids which have only one genome, and also noted a high correlation between the number of bivalents and the number of bridges at anaphase I or II. The presence of bridges would suggest that crossing-over must have taken place between completely non-homologous chromosomes. Since no bridges were observed in this study, and since normally disjoining bivalents were frequently noted, it must be assumed that pairing occurred between partially homologous chromosomes. If the presence of bridges is a true indication of intra-genome pairing, then their complete absence could indicate equally well, inter-genome pairing.

While mostly open bivalents were observed, a closed pair with a chiasma on both sides of the centromere was observed in three cells, Figs. 7 and 8. So far as is known, this has never been observed in any of the haploids that have been studied. Such complete pairing certainly suggests even greater homology between the various chromosomes than has usually been assumed to exist.

Secondary pairing, while frequently observed, is not likely an indication of true homology. Possibly as Bleier (2) has suggested, stickiness of the chromosomes from prophase on, could account for its occurrence. Gene specificity or chemical attraction between chromosomes may also be a suitable explanation for the formation of secondary pairs.

As mentioned previously, the random distribution of the chromosomes at anaphase I, was obviously restricted. Bivalent formation and secondary associations were likely responsible for disturbing the distributions. Regular disjoining of bivalents at anaphase I would alone be restrictive, but also the secondary associations remained united going to the same pole, thereby further affecting normal distribution. It is, therefore, concluded that distribution was random when 21' were present, but that when pairing did occur, distribution was random for only those chromosomes not involved in the pairing.

Chains

Associations or chains of three to five univalents were observed in 4.5% of the cells, Fig. 9. Apparently a continuation of secondary pairing was responsible for this type of chain formation. These associations would likely go to the same pole, thereby further affecting the randomness of chromosome distribution.

Cells with Reduplicated Chromosomes

One cell was observed that had 21" at metaphase I, Fig. 10. So far as could be determined, such a phenomenon has never

been observed in any of the haploids that have been studied. Pairing was normal and very likely normal gametes would result from such a cell. Seven cells were observed that had 42 mostly univalent chromosomes, Fig. 11. It is postulated that the first type of reduplicated cell could have arisen from failure of cell wall formation during the first mitotic division of a sporogenous cell. When the nuclei so formed, prepared for the second mitotic division, a common spindle was formed and the resulting daughter cells (microsporocytes) would have 42 chromosomes each. Meiosis would then proceed normally. In the second case, cells with 42 univalents could have arisen by cell wall failure in the second mitotic division (immediately preceding microsporocyte formation). Since the nuclear membranes in these binucleate cells would remain intact until diakinesis, there would be no opportunity for the 42 chromosomes to pair.

Only five cells contained dyads, Figs. 12 and 13, which were probably formed from a first division split of the univalents, remaining joined only at the centromere. In Fig. 12 it can be seen that some of the univalents have undergone complete splitting and the monads and dyads are being randomly distributed to the poles. It is probable that the dyads would undergo a second division but the gametes thus formed would be deficient for several whole chromosomes rendering them non-functional.

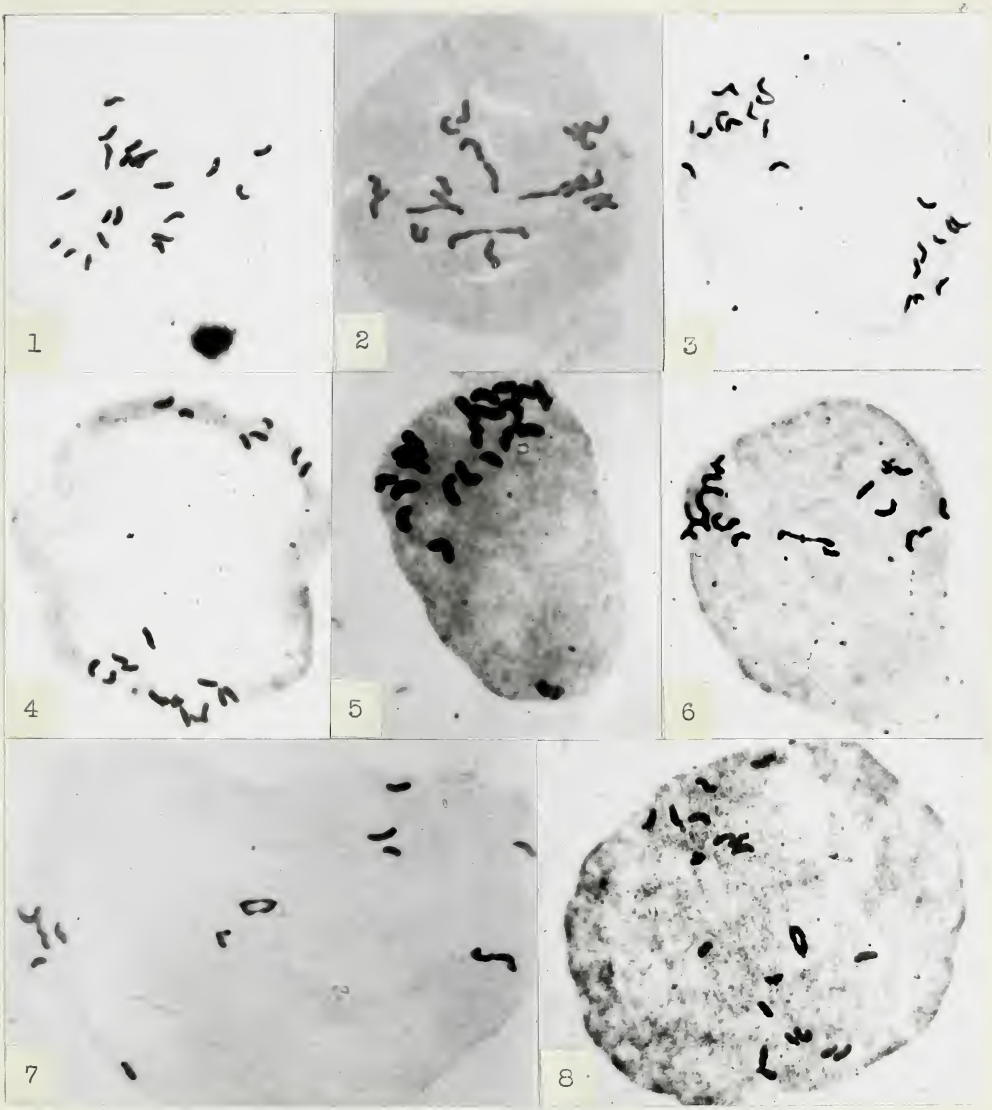


Plate I

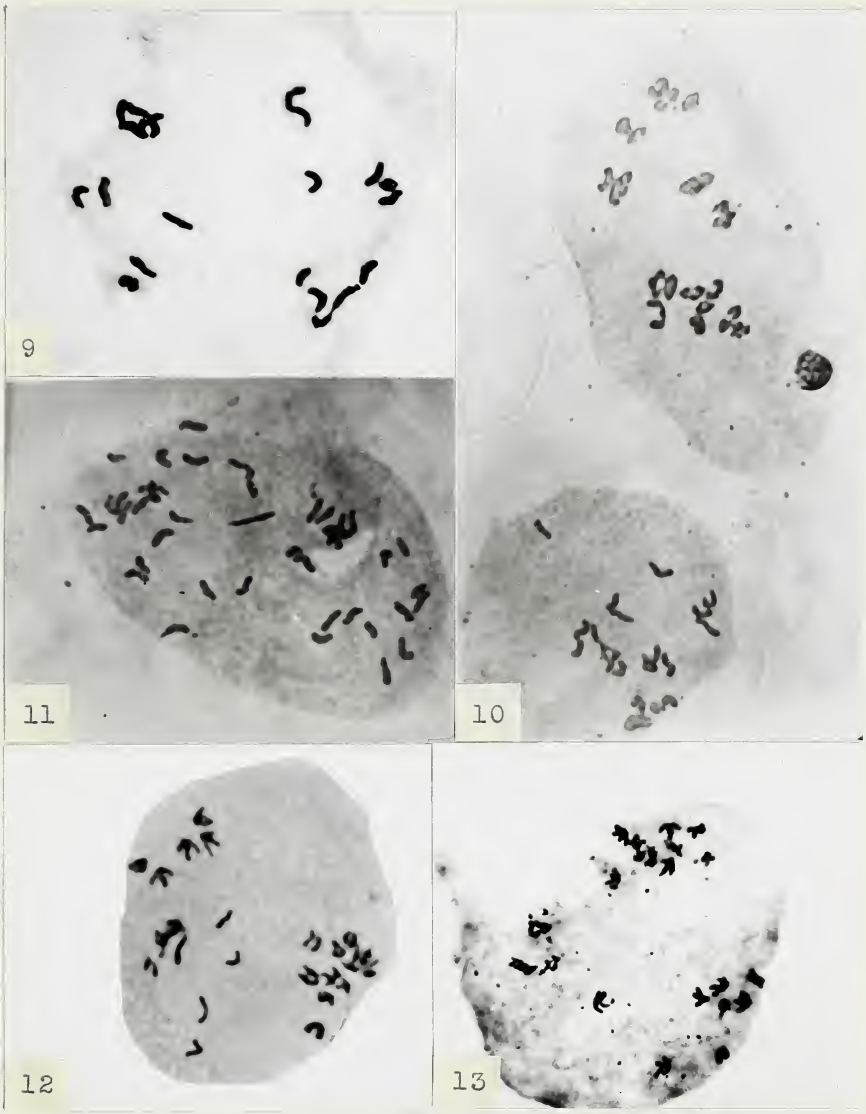


Plate II

Legend to Plates I and II

Microsporogenisis in the haploid.

Fig. 1. Metaphase I. Distribution of the 21 unpaired chromosomes throughout the enitre cell.

Fig. 2. Metaphase I. Distribution of univalents with two bivalents and secondary pairing.

Figs. 3, 4 and 5. Anaphase distributions; 12-9, 14-7 and 20-1, respectively.

Fig. 6. 19'1". Open bivalent with strong chiasma.

Fig. 7 and 8. Closed bivalent.

Fig. 9. Chain associations.

Fig. 10. Cell with 21 normal pairs; a second cell with 21 univalents.

Fig. 11. Cell with 42 mostly univalent chromosomes.

Fig. 12. Monads and dyads.

Fig. 13. A 14-7 distribution of dyads.

Magnification:

Figs. 2, 5 and 9 at 900 diameters; all others at 720 diameters.

CYTOLOGICAL DATA FROM THE F_2 AND F_3 GENERATIONS

Since no cytological data are available from the F_1 plants, all information on the transmission of aberrations had to be obtained from the analyses of the F_2 and F_3 populations. The chromosomal constitutions of the F_2 and F_3 generations which were cytologically examined, are presented in Table 3.

Of the 60 F_2 plants examined, 26 or 43% had a normal chromosomal complement of 21", Fig. 15. Of 231 F_3 plants examined, 153 or 66% proved to have a normal constitution. Consequently, these data indicate that plants with chromosomal aberrations became progressively fewer with succeeding generations. As would be expected, all normal F_2 plants had normal progeny. Aberrant plants, however, transmitted aberrations to some of their offspring. Furthermore, the aberrations varied markedly in different sister progenies, being in some cases more extreme than in the parent. Apparently the degree of abnormalness of the parent plant determined the relative frequency of normal and abnormal progeny.

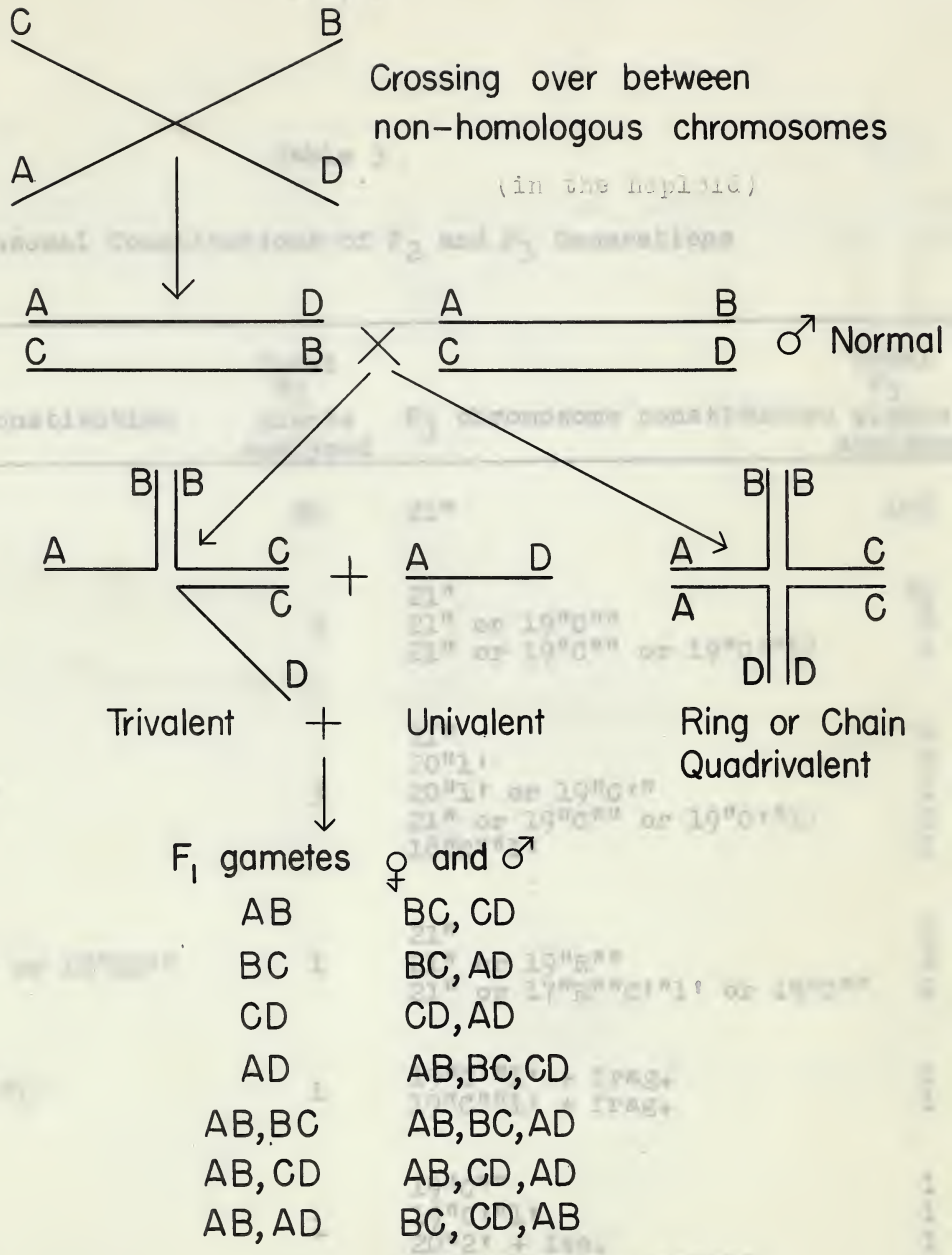
The most common type of aberrations noted were chains of three or four chromosomes, rings of four and univalents. It is assumed that these aberrations were largely the result of reciprocal translocations that occurred in the haploid. Moreover, the high

frequency of F_2 and F_3 plants containing up to three associations of three or four chromosomes, further substantiated the hypothesis that up to three reciprocal translocations occurred in the haploid. Disjunction from translocation configurations likely caused the formation of deficient and duplicated gametes which would result in plants having chains and also unpaired chromosomes, especially if the interchanged portion were small. A diagramatic representation of the probable origin of aberrant gametes from one reciprocal translocation, is presented in Fig. 14. Random union of any two of such gametes, gives numerous possibilities for various types of chromosomal aberrations. If as many as three reciprocal translocations were involved, the resulting progeny could have all the cytological abnormalities observed in this study, Figs. 16 to 25. It is probable that most male gametes would be normal in chromosome number, but occasionally ones with an aneuploid number might be functional. Female gametes, on the other hand, would be expected to transmit aberrations with a fairly high frequency.

The total number of chromosomes in different fertile plants ranged from 39, Fig. 16, to 47, Fig. 17. It is surprising that fertility and vigor was high even in some of the most aberrant plants. The plant with 39 chromosomes appeared quite normal phenotypically. This is highly interesting since Sears (21) found that nullisomics were usually quite weak and sterile. Probably the 39

chromosome plant had certain interchanged chromosomes so that there was actually no complete absence of essential genetic material.

The meiotic behaviour of one F_3 plant should be especially noted, Fig. 26. At metaphase I, it proved to be highly asynaptic similar to nulli-3 described by Sears (22). It is possible that this plant was nullisomic for chromosome three, and the origin of such a plant also can be explained from the union of certain gametes, each deficient for the same chromosome, Fig. 14.



F_2 Deficiencies and duplications associated with univalents, bivalents, trivalents and quadrivalents would occur. These aberrations would be transmitted to subsequent generations.

Fig. 14 Diagramatic representation of the probable origin

F_1 gametes	♀ and ♂
AB	BC, CD
BC	BC, AD
CD	CD, AD
AD	AB, BC, CD
AB, BC	AB, BC, AD
AB, CD	AB, CD, AD
AB, AD	BC, CD, AB

F_2 Deficiencies and duplications associated with univalents, bivalents, trivalents and quadrivalents would occur. These aberrations would be transmitted to subsequent generations.

Table 3

Chromosomal Constitutions of F_2 and F_3 Generations

F_2 chromosome constitution	Total F_2 plants analysed	F_3 chromosome constitution	Total F_3 plants analysed
21"	26	21"	108
21" or 19"C""	9	21"	24
		21" or 19"C""	8
		21" or 19"C"" or 19"C:"1:	1
21" or 19"C:"1:	3	21"	6
		20"1:	2
		20"1: or 19"C:"	1
		21" or 19"C"" or 19"C:"1:	3
		18"C""1:	1
21" or 19"C:"1: or 18"2C:"	1	21"	3
		21" or 19"R""	2
		21" or 17"R""C:"1: or 19"C""	1
19"C"" or 19"C:"1:	1	19"C:"1: + frag.	1
		19"C""1: + frag.	1
18"C""2:	1	19"C""	1
		19"C:"1:	1
		20"2: + iso.	1
		17"C""C:"1: or 19"C""	1
19"C:" or 17"2C:"1:	1	-	0
16"C""C:"3:	1	19"C:"1:	3
		18"C""2:	1
		17"C:"4:	1
		16"3C:"3:	1

Table 3 (Continued)

F_2 chromosome constitution	Total F_2 plants analysed	F_3 chromosome constitution	Total F_3 plants analysed
20"1'	4	21"	6
		20"1'	9
		19"2'	1
20"1' or 19"3' or 18"C""1'	1	20"1' or 19"C'" or 19"3'	1
		19"2'	2
19"3'	1	21"	1
		20"1'	1
		19"2'	1
19"2'	2	20"1'	3
		19"1'	3
		19"2'	1
17"C'"3'	1	20"1' or 19"C'"	1
		20"1'	2
		19"3'	1
15"C'"2'2 + iso.	1	-	0
21"1' or 19"R""1'	2	21"1' or 20"C'"	1
		20"1' or 19"C'"	2
		19"4' or 18"C""2'	1
		18"C""1' or 17"C""3' or 20"1'	2
		18"C'"2'	1
		21"	1
21"2' or 20"C"" or 20"4'	1	21" "	3
		21"2' or 20R""	1
		20"R""C'" or 18"2r""C'"	1
		19"C""1' or 18"C""C'" or 15"C""2C'"3'	1
		19"C"" or 19"C'"1'	1
19"c'"3' or 18"2C'"2'	1	-	0
21"1' or 20"C'" or 18"C""C'"	3	21"1' or 20"C'"	7
		19"C""1'	2
		21" + frag.	1
		21"	1
Total	60		231

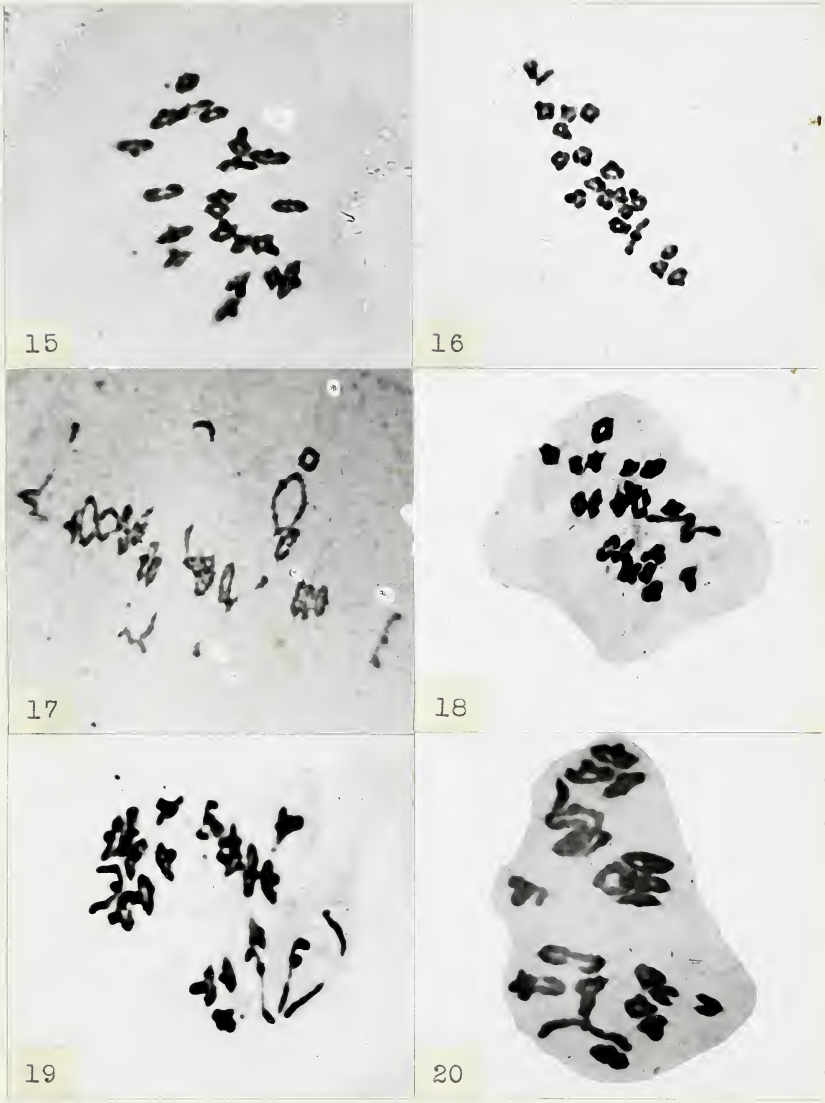


Plate III

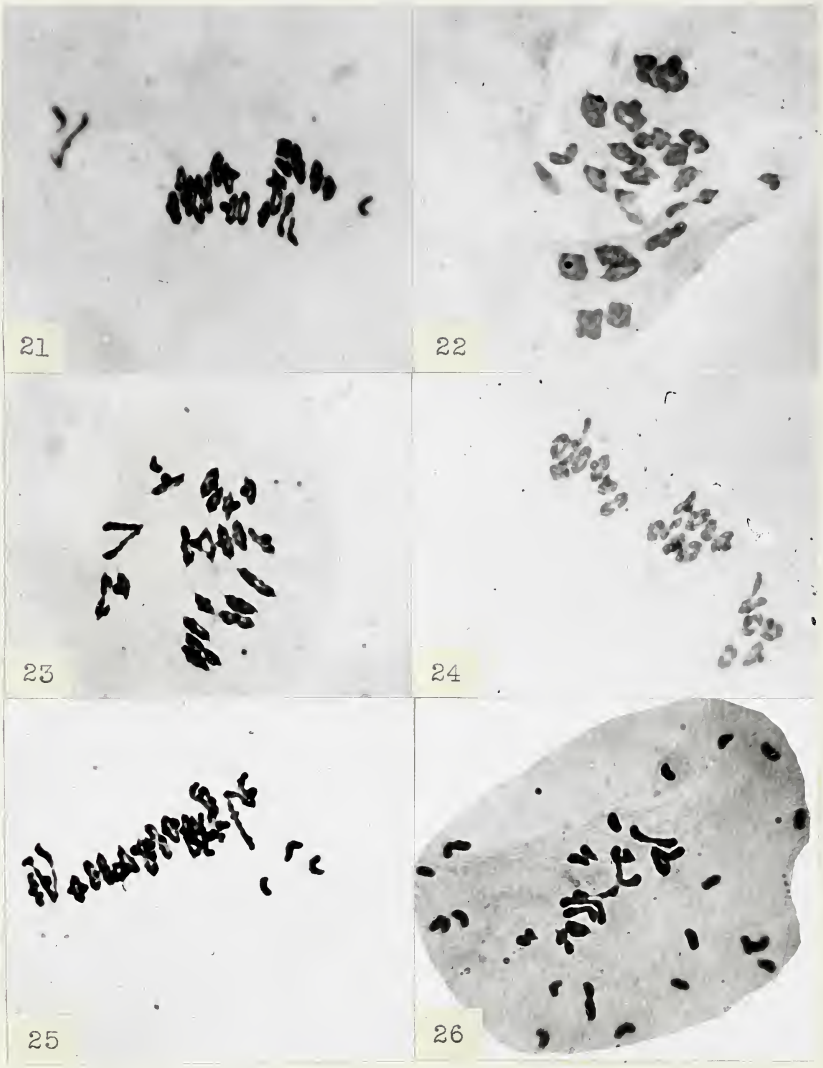


Plate IV

Legend of Plates III and IV

Microsporocytes of F_2 and F_3 Plants.

Fig. 15. Cell with 21".

Fig. 16. F_3 cell with 19"1'.

Fig. 17. F_3 cell with 18"2R""C'".

Fig. 18. and Fig. 19. F_2 and F_3 cells with 19"C"".

Fig. 20. F_2 cell with 19"R""1'.

Fig. 21. F_2 cell with 17"2C'"1'.

Fig. 22. F_2 cell with 19"2'.

Fig. 23. F_3 cell with 19"C'"1'.

Fig. 24. F_3 cell with 19"C'".

Fig. 25. F_3 cell with 16"3C'"3'.

Fig. 26. F_3 cell. Highly asynaptic.

All figures at a magnification of 720 diameters.

CONCLUSIONS

It is concluded that the pairing observed in the haploid occurred between chromosomes because of homology rather than translocation heterozygosity. This pairing, however, resulted in reciprocal translocations which gave rise to plants in succeeding generations, with various deficiency and duplication constitutions. These results are interpreted as evidence that there is considerable homology between chromosomes of the various genomes in hexaploid wheat. It is highly probable, of course, that the actual gene homology and duplication present in common wheat haploids, is much greater than the actual pairing indicated. Pairing would likely occur only when considerable portions of chromosomes were identical. In the evolution of this species it is likely that many gene and chromosome rearrangements have occurred so that while there is genetic homology, there is structural homology for meiotic pairing in only relatively few haploid chromosomes.

It is felt that secondary pairing is no indication of true chromosomal homology, but that it restricted random distribution of the chromosomes to the poles. The same process causing secondary pairing was likely also responsible for the formation of chains.

Cells with reduplicated chromosomes were found and it is suggested that the process whereby these were formed could account for the formation of doubled gametes and seed setting in normally sterile hybrids. In the case of the cell with 21", it is assumed that cell wall formation failed during the first mitotic division of the sporogenous cell, while in the case of cells with 42', cell wall formation failed in the second mitotic division.

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